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SOME EXPERIMENTS IN MASS SELECTION

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AT the close of an interesting review of "seventeen years selection" of the character winter egg production in Barred Plymouth Rock fowls, made at the Maine Agricultural Experiment Station,¹ Dr. Pearl compares his results with those of Phillips and myself² in selecting for a like number of generations the hooded pattern of rats and concludes that the same interpretation should be given to both series of experiments, viz., that selection can change a population but not a character.

Without discussing for the moment the validity of the now world-famous generalization of Johannsen, which Pearl here accepts for his fowls and seeks to extend to our rats, I wish to point out some differences between the two cases which make a direct comparison between them difficult and conclusions based upon them of unequal validity.

The character winter egg production in fowls is on Pearl's showing extremely difficult to determine. It is necessarily an unknown quantity in all male birds, which themselves produce no eggs, and any influence which

¹ "Seventeen Years Selection of a Character Showing Sex-linked Mendelian Inheritance," AMERICAN NATURALIST, Vol. 49, pp. 595-608, 1915.

² "Piebald Rats and Selection," Publ. No. 195, Carnegie Institution of Washington, 1914.

males may exert on the egg-production of their daughters can be tested only by an indirect and rather uncertain process. Only in the case of females is the character directly measurable and then only for such females as (1) are hatched "after April 1 and before June 1," (2) survive all the accidents of chickhood and adolescence, (3) escape all attacks of disease and are kept continuously free from parasites, and (4) are properly fed and housed. For any bird which dies, is disabled or becomes seriously ill under ten months old, the character is an unknown quantity. These limitations make the proportion of birds which can be accurately rated as regards the character extremely small, and reduce correspondingly the material on which selection can be practised.

Contrast with this situation that regarding the hooded pattern of rats. This character is possessed by every individual of both sexes and is inherited equally through either sex. The character is fully developed in its final form within a week after birth, months before sexual maturity is attained. This makes it possible to grade the animals accurately while they are still very young and to discard at once all individuals which fall below the adopted standard. Selection thus has a vastly greater amount of material to work with, and the variation in each generation can be ascertained with a completeness and accuracy quite impossible in the case of winter egg production in fowls.

It is scarcely necessary to point out that upon the completeness of one's knowledge of the character and extent of variation depends his ability to take advantage of that variation by systematic selection. By this criterion winter egg production is very poor material on which to base an experimental test of "mass selection," whereas the hooded pattern of rats is material admirably adapted for the purpose. Many times has the fact been commented upon that Mendel's fortunate choice of peas as material for his studies of hybridization was largely responsible for his success where others failed. If one wishes to test

a theory he must choose material suited to the purpose. No adequate test of the efficacy of mass selection can be obtained from material which can not be accurately judged in the mass.

Pearl points out further limitations of his material in the statement "that phænotypic variation of the character fecundity, in fowls, markedly transcends, in extent and degree, genotypic variation." That is, non-heritable causes of fecundity are in excess of heritable causes and serve to obscure the occurrence of the latter. Further, Pearl says:

It is quite impossible in the great majority of cases to determine with precision what is a hen's genetic constitution with respect to fecundity from an examination of her egg record alone.

If then one has reared his pullets to the age of one year, has kept them free from disease and parasites, has fed and housed them properly and has even trap-nested them and recorded their eggs all winter, still he has no sufficient basis on which to base a selection. He must first rear and test their progeny in the same way. Pearl's statements on this point, the accuracy of which I do not question, are sufficient to show the entire unsuitability of his material for testing the efficacy of mass selection.

One might with propriety even question whether such a thing as inherited capacity for winter egg production exists in fowls, but on this point, I think, another investigation³ made by Pearl is conclusive, in which he crossed Cornish Indian game fowls, which are poor winter layers, with Barred Plymouth Rocks which are fairly good winter layers. Reciprocal crosses were made in both of which the daughters showed resemblance to the racial winter egg productiveness of the sire's race. This result indicates that a sex-linked genetic factor of some sort exists which affects winter egg production in fowls. But since the fecundity of the offspring was obviously influenced by the mothers' race as well as by the father's race, Pearl was

³ "The Mode of Inheritance of Fecundity in the Domestic Fowl," *Jour. Exp. Zool.*, Vol. 13, p. 153, 1912.

led to suggest the existence of a second fecundity factor which was *not* sex-linked. He assumes that this second factor, like the first, is a Mendelizing factor, but without any sufficient published evidence for either conclusion. To this I called Dr. Pearl's attention soon after the publication of his paper and suggested that if possible the data be put on record in such form as to allow of testing this and other hypotheses concerning the genetic factors concerned. For one-factor, two-factor, ten-factor and infinity-factor Mendelian hypotheses would call for very different ratios and distributions of fecundity among the offspring. He replied that the data could not be so given without an amount of work which he considered unprofitable. We are left, therefore, with only this information concerning Pearl's pullets, whether each one laid *more* or *less* than 30 eggs in its first winter. If we knew *what* number each one laid, we might form an intelligent opinion as to whether Mendelian factors are involved, and if so how many, in the same way that we can test Mendel's conclusions concerning the independent inheritance of yellow cotyledon color and round seed form in peas because he tells us the actual proportions of the various sorts of peas reported for each plant. Being denied such information by Pearl, it is useless to discuss his two-factor hypothesis, for its correctness can be neither proved nor disproved.

Leaving aside the question whether any inherited *factor* has changed as a result of selection in Pearl's experiments, which we have no means of investigating, we can consider only the question whether the gross winter egg production has changed. As a basis for judgment he gives us the averages of winter egg production year by year for sixteen years. Pearl's graphic presentation of the data (assuming that the considerable fluctuation recorded is not significant) indicates a steady decline of the general flock average during the first nine years of the experiment and a steady recovery and further increase during the next seven years, which he ascribes to

the different basis of selection in the two periods. But it is hard to believe that this entirely explains the difference in result. One notices for example that during the period of ostensible decline the highest average fecundity (45.23) is recorded when the number of birds under observation is smallest (48) and the lowest average (19.93) is recorded when the flock is largest (780). Further, in the later seven-year period of "improvement," the number of birds tested declines as their average fecundity rises. Has not the better environment and lessened competition of small numbers possibly something to do with the changes noted? Is it certain that genetic agencies are responsible for the differences observed? Pearl himself nowhere states that the selection practised during the earlier period had produced positive deterioration; he merely states that "there was no change of the mean in the direction of the selection" during this period when selection was based on high production without progeny tests. But as soon as progeny tests were made an additional feature of the basis for selection Pearl notes immediate results, viz., the immediate isolation of a strain which in its first year made a record for high productiveness only once equalled in the six subsequent years. How many successive selections were made in this period, we are not informed, but since it would require at least two years to make a combined performance and progeny test, it would seem that not more than three successive selections can have been carried out on this basis in the seven year period from 1908 to 1915. It may fairly be questioned whether this is an adequate test of the effectiveness of mass selection. The total number of individuals tested during this period is, according to Pearl's table, 1,655. For the entire seventeen years of selection it is 4,842.

The total number of animals graded in our selection experiments with rats heretofore published is 20,645, and the number of generations involved 13. Since those figures were compiled, four additional generations of

rats have been reared in the straight selection series, bringing the total number of animals observed in this experiment up to 33,249, and the total number of generations of selections up to 17, numbers certainly more nearly justifying the term "mass selection" than those studied by Pearl. As no previous account of this experiment has been given to readers of the NATURALIST, a brief review of its salient features may be appropriate here.

Experiments made by MacCurdy and by Doncaster had shown that the hooded pattern of rats is a Mendelian recessive character dominated in crosses by the "self" or entirely pigmented condition of wild rats and of certain tame races. The F_2 ratio obtained in crosses between hooded and self rats is an unmistakable monohybrid ratio, viz., 493 hooded: 1,483 self, or 24.9 per cent. hooded. The hooded pattern is subject to slight fluctuations in the relative amounts of pigmented and unpigmented surfaces, and though these slight plus and minus variations are such as are usually disregarded in Mendelian analyses, MacCurdy's investigations had indicated that they are to some extent inherited. It was our purpose in starting the selection experiments to ascertain whether the observed fluctuations were capable of increase and summation through the action of repeated selection, a possibility denied for all such cases by de Vries and Johannsen on theoretical grounds and quite incompatible with notions prevailing then as to the "gametic purity" of recessives. This "pure line" idea Pearl still maintains on the basis of his observations of the winter productiveness of his pullets. But, as I have tried to show, his material is no more adequate than that of Johannsen, which involved no demonstrated Mendelian character whatever. For, though Pearl *assumes* that winter egg productiveness of fowls involves a "sex-linked Mendelian character" he has withheld from publication the only facts on which such an assumption may legitimately be based.

Our selection experiments with hooded rats began in

1907. The initial stock consisted of less than a dozen individuals all "pure recessives," which produced only "recessive" hooded young, in accordance with Mendelian expectation. But though all the young were recessive (hooded), all were not exactly alike, and to assist in their classification we devised arbitrary "grades" of increased (plus) or decreased (minus) pigmentation as compared with the *modal* (zero) condition in our hooded race. The scale of "grades" is shown in part in Fig. 1. It has

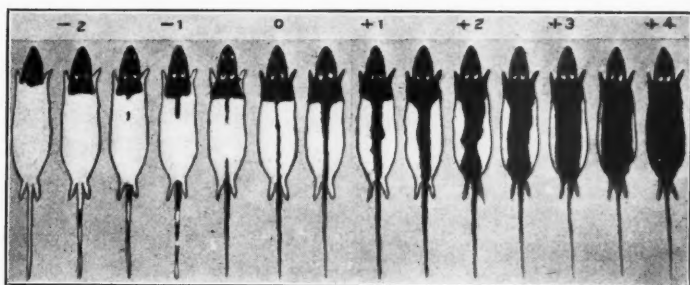


FIG. 1. Arbitrary set of grades used in classifying the fluctuating variations of hooded rats.

been found necessary to extend it in both directions, beyond the range shown in the figure, in order to admit the new grades of rats which have made their appearance as the experiment progressed. The first plus-selected parents produced 150 offspring ranging in grade from +1 to +3, mean +2.51. The first *minus-selected* parents produced 55 offspring ranging in grade from -2 to +1, mean -1.46. It will be observed that the ranges of the young produced in the two selections were practically continuous with each other, though they did not actually overlap. But actual overlapping did occur in the following generation, in which no advance was made in the mean grade of the parents, practically all the available females being used as parents in an effort to increase the stock. The grade of the offspring also remained practically stationary in this second generation (see Tables I

TABLE I

RESULTS OF THE PLUS SELECTION OF HOODED RATS CONTINUED THROUGH
SIXTEEN SUCCESSIVE GENERATIONS

Generation	Mean Grade of Parents	Mean Grade of Offspring	Lowest Grade of Offspring	Highest Grade of Offspring	Standard Deviation of Offspring	Number of Offspring
1	2.51	2.05	+1.00	+3.00	.54	150
2	2.52	1.92	-1.00	+3.75	.73	471
3	2.73	2.51	+ .75	+4.00	.53	341
4	3.09	2.73	+ .75	+3.75	.47	444
5	3.33	2.90	+ .75	+4.25	.50	610
6	3.52	3.11	+1.50	+4.50	.49	861
7	3.56	3.20	+1.50	+4.75	.55	1,077
8	3.75	3.48	+1.75	+4.50	.44	1,408
9	3.78	3.54	+1.75	+4.50	.35	1,322
10	3.88	3.73	+2.25	+5.00	.36	776
11	3.98	3.78	+2.75	+5.00	.29	697
12	4.10	3.92	+2.25	+5.25	.31	682
13	4.13	3.94	+2.75	+5.25	.34	529
14	4.14	4.01	+2.75	+5.50	.34	1,359
15	4.38	4.07	+2.50	+5.50	.29	3,690
16	4.45	4.13	+3.25	+5.87	.29	1,690
						16,107

TABLE II

RESULTS OF THE MINUS SELECTION OF HOODED RATS CONTINUED THROUGH
SEVENTEEN SUCCESSIVE GENERATIONS

Generation	Mean Grade of Parents	Mean Grade of Offspring	Lowest Grade of Offspring	Highest Grade of Offspring	Standard Deviation of Offspring	Number of Offspring
1	-1.46	-1.00	+ .25	-2.00	.51	55
2	-1.41	-1.07	+ .50	-2.00	.49	132
3	-1.56	-1.18	0	-2.00	.48	195
4	-1.69	-1.28	+ .50	-2.25	.46	329
5	-1.73	-1.41	0	-2.50	.50	701
6	-1.86	-1.56	0	-2.50	.44	1,252
7	-2.01	-1.73	0	-2.75	.35	1,680
8	-2.05	-1.80	0	-2.75	.28	1,726
9	-2.11	-1.92	- .50	-2.75	.28	1,591
10	-2.18	-2.01	-1.00	-3.25	.24	1,451
11	-2.30	-2.15	-1.00	-3.50	.35	984
12	-2.44	-2.23	-1.00	-3.50	.37	1,037
13	-2.48	-2.39	-1.75	-3.50	.34	1,006
14	-2.64	-2.48	-1.00	-3.50	.30	717
15	-2.65	-2.54	-1.75	-3.50	.29	1,438
16	-2.79	-2.63	-1.00	-4.00	.27	1,980
17	-2.86	-2.70	-1.75	-4.25	.28	868
						17,142

and II). In the third and all subsequent generations selection was made as rigorous as possible consistent with the maintenance of a strong colony from which to make further selections. Following each selection an advance in the average grade of the offspring took place attended by a steady movement in the direction of the selection on the part of both the upper and the lower limits of variation. The sixteenth plus selection produced 1,690 offspring (a larger number of individuals than is contained in Pearl's entire seven-year series) *every one of which fell beyond the original range of variation*, which was from $+1$ to $+3$ in the first plus selected generation and from $+3\frac{1}{4}$ to $+5\frac{1}{2}$ in the sixteenth generation. What this change signifies will be better appreciated when I state that $+6$ in our grades is a wholly pigmented or "self" rat, and that the extreme variation noted, $+5\frac{1}{2}$, signifies a rat wholly pigmented except for a few white hairs between the front legs. The *whole race* has accordingly been changed so that *no individual* is longer produced which falls within the original range of variation. Not a dozen rats in this entire generation would be allowed by a fancier in the category of "hooded" rats.

In the minus selection series the results secured are scarcely less striking. Only a very few individuals of the 1,980 sixteenth generation rats, or the 868 seventeenth generation rats fell within the original range of variation, which in generations 1-3 went no farther than grade -2 . In all other individuals of the sixteenth and seventeenth generations the "hood" was reduced to an extent never seen in the hooded rats of the fancier, the white areas having covered the neck and in extreme cases the forehead also, leaving only the nose and a patch round the eyes and ears still pigmented.

Pearl (p. 607) commenting on the results of his selections states that he had no reason to think that at the close of the series any individual had been produced superior in productiveness to those which occurred at the outset, but that he had merely secured *more of them*, thus raising

the average. With the rats, however, a very different condition exists. The average is not changed by increase of high-grade individuals merely or chiefly. At the present time *every individual* in the plus selection series and *nearly every individual* in the minus selection series is of higher grade (plus or minus respectively) than *any* individual in the race at the outset. It is not a fallacious change of averages which has taken place; a genuine and permanent racial change has occurred, following step by step upon repeated selection. Generation by generation new grades of offspring have come into existence, more extreme in character than any which existed before, and simultaneously with the advance of the outer limit of variation the inner limit has receded. No great change in variability has attended the selection. The standard deviation has decreased somewhat to about three fifths of its original amount, but has scarcely altered in the last eight or ten generations (see Tables I and II). Rather there has occurred a change in the *modal condition* of the character, about which fluctuation continues very much as before. When the position of the mode changes, as a result of selection, the position of the average and of the upper and lower limits of variation change with it. In a word the *character* changes.

In our 1914 publication Phillips and I were conservative about asserting a change in the single Mendelian unit-character manifestly involved in the hooded pattern. We suggested the possibility that other as yet undiscovered factors might be responsible for the apparent changes observed and awaited the result of experiments then in progress to show whether such a possibility was admissible. I have no hesitation now in saying that it is not. All the evidence we have thus far obtained indicates that outside modifiers will not account for the changes observed in the hooded pattern, itself a clear Mendelian unit. We are forced to conclude that this unit itself changes under repeated selection *in the direction of the selection*; sometimes abruptly, as in the case of our "mu-

tant" race, a highly stable plus variation; but much oftener gradually, as has occurred continuously in both the plus and the minus selection series. The permanency of these cumulative changes we have tested by repeated crossing of both selected races with the same wild race. The first cross seems to undo to a slight extent the work of selection, causing regression in both plus and minus selected races, but a second back cross with the wild race causes no further regression. Thus, plus-selected rats of mean grade 3.45 were crossed with wild rats and the recessive character was recovered in F_2 in 75 individuals, 24 per cent. of the entire generation. These 75 extracted hooded rats were of mean grade 2.89, a regression of .56 on the mean grade of their hooded grandparents, which is about double the regression shown by the plus selected race when not crossed with wild rats. It seems proper therefore to attribute to the wild cross a part of the regression observed in this case and this I have expressed by saying that crossing the selected race with wild rats tends to *undo* the work of selection. The suggestion was tentatively adopted by Phillips and myself that this *undoing* consisted in the removal of "modifiers" of some sort, possibly independent Mendelizing factors. If this explanation were correct, further crossing with wild rats should tend still further to "undo" the work of selection, so that ultimately the extracted hooded race should return completely to its original modal state, the zero grade. To test this matter, extracted hooded rats ranging from grade $+2$ to $+4$ (mean grade 3.01) were crossed back a second time with pure wild rats. The theory of independent modifiers would lead one to expect further regression as a result of this cross, but no regression was this time observed. Instead an advance of .32 took place bringing the mean of the twice extracted hooded recessives back to about the grade of the uncrossed race. The mean grade of the once-extracted grandparents, loaded in proportion to the number of their twice-extracted hooded grandchildren, was 3.01; the mean of the 263 hooded grandchildren was 3.33.

The number of these grandchildren is large enough to leave no doubt as to the conclusion that no further regression attended extraction of the hooded character a second time from the wild cross. The proportion of hooded individuals to non-hooded is also an unmistakable monohybrid ratio, viz., 263 hooded to 759 non-hooded, or 25.7 per cent. hooded in a total of 1,022 individuals.

This result indicates clearly the untenable character of our provisional hypothesis to explain the altered grade of hooded rats under selection and crossing, by invoking the action of independent modifying Mendelian factors. No evidence is forthcoming from further and more extensive experiments that such modifying factors are concerned in the result. It seems rather that the hooded character, which is a mosaic or balanced condition of pigmented and unpigmented areas, is slightly unstable. It oscillates regularly about a mean condition or grade, these oscillations being not phenotypic merely but in part genotypic so that selection brought to bear upon them is immediately and continuously effective.

There may exist cases of continuous variation purely phenotypic, as that of Johannsen's beans seems on his showing to be. In other cases phenotypic variations may so largely exceed genotypic variations that it is difficult to discover and isolate the latter, as has been Pearl's experience. But our experiments with rats show beyond reasonable doubt that genotypic variation, as well as phenotypic, may assume a continuous form, and if it does no one can question its further modifiability by selection. In denying effectiveness to selection in the case of continuous variation, it has been assumed, tacitly by DeVries and expressly by Johannsen, that continuous variation is wholly phenotypic. This assumption being disproved, the pure-line theory which rests upon it lacks adequate support.

It seems strange looking backward that the idea should have become so widely accepted that continuous or fluctuating variations are wholly phenotypic. For a continu-

ous variation signifies only the combined result of several independent agencies. In purely phenotypic variation (such as possibly Johannsen has observed) these agencies are obviously environmental and so do not affect the inheritance. But in a case of multiple genetic agencies (the existence of which everyone recognizes) a continuous series of variations may result which would be amenable to selection. Pearl and all other pure-line advocates admit the existence of such cases. But the same thing would result if, aside from purely phenotypic variations in a character, its single factorial basis should undergo quantitative variation. It is precisely this last named category of cases which alone can explain our rat results. And it is precisely this category of cases which the pure-line advocates, unable to disprove, boldly deny. Driven from all other defences they cling to this as their last line and solemnly repeat challenges issued years before in moments of greater confidence. Thus Pearl closes his paper with a renewal of the opinion expressed by him in 1912.

It has never yet been demonstrated, so far as I know, that the absolute somatic value of a particular hereditary factor or determinant (*i. e.*, its power to cause a quantitatively definite degree of somatic development of a character) can be changed by selection on a somatic basis, however long continued.

Our observations on rats are submitted as a sufficient answer to this challenge.

I do not suppose that Pearl means to be taken seriously when he says (p. 608):

The extreme selectionist appears to believe that in some mysterious way the act of continued selection, which means concretely only the transference of each selected individual from one cage or pen to another to breed, will in and of itself change the germ-plasm.

I have never heard a selectionist, however extreme, express such a view; certainly I, whose views are attacked in the next sentence, have never entertained such an idea. But Dr. Pearl knows, as well as I do, that while the germ-plasm of the individual remains unmodified upon its trans-

fer from one cage to another, the character of the *germ-plasm of its descendants*, and so of the race, depends very largely upon what mates are transferred to the same cage with it. This is where the selection comes in and there is nothing "mysterious" about it either.

The idea that selection can bring about no change in the germ-plasm of the race "except by sorting over what is already there," to which Pearl gives expression, rests on the assumption that the germ-plasm never changes. What ground have we for such an assumption? No more than for the idea of the unchangableness of species, which formerly prevailed. Even Johannsen admits that large germinal changes ("mutations") *sometimes* occur. He himself records having observed them. Why should we be so skeptical about the occurrence of minor germinal changes? It is easy to overlook them when purely somatic changes are associated with them and outnumber them as they possibly do in Johannsen's beans and Pearl's fowls but a single clearly established case should suffice to establish their existence and their importance in evolution.

THE INHERITANCE OF BLACK-EYED WHITE SPOTTING IN MICE

C. C. LITTLE

BLACK-EYED white varieties of rodents have long been recognized and used as material for genetic investigation.

Cuénot, Morgan and Durham with mice and Castle with guinea-pigs have utilized this particular color variety in breeding experiments. For the most part they are agreed that black-eyed white varieties represent an extreme condition of the ordinary "spotted" or "piebald" series.

Cuénot (1904) in treating the inheritance of spotting concludes that there exists a continuous series of partially pigmented forms extending on the one hand from mice with white on the tail, or with a small white ventral patch, or with small white forehead spot, through a series of decreasingly pigmented forms until the black-eyed white form is reached at the other end of the series. As to a factorial explanation for the phenomena observed in the inheritance of spotting, Cuénot feels that there are numerous stages of the spotted condition (P) which he designates by p^1 , p^2 , p^3 , p^4 as progressively whiter forms are considered. He believes, however, that the details of spotting are not represented in the germ cell. He further mentions the failure to obtain any particular stage of spotting in a true breeding condition. Selection of nearly solid-colored forms has enabled him to obtain animals with greatly increased white areas.

Durham (1908) has obtained some evidence for two different types of spotting, one recessive to solid-coated forms and one dominant to them. She has reported several crosses which I have considered in more or less detail in another paper (Little, 1914). None of the crosses presented by her can be considered as critical tests of the presence of two distinct spotting factors. Morgan (1909),

who has worked with the same types as Durham, feels uncertain as to the real significance of black-eyed whites and as to the occurrence of a distinct factor for dominant spotting. This uncertainty I also felt and have tried to show further reasons for not considering Miss Durham's work as establishing the existence of a dominant spotting factor.

Castle (1905) has found that in guinea-pigs black-eyed whites behave in inheritance in much the same way that the same type of mouse behaves, namely that black-eyed whites do not breed true but give, when crossed *inter se*, a whole range of spotted forms in addition to some like themselves.

One can by selection progress in either direction through a series of spotted forms, decreasing or increasing the number and extent of pigment patches. Great difficulty, however, was encountered in trying to fix the color pattern at any particular stage in the series. Up to the present time this has not been proved possible.

EXPERIMENTAL

In the early winter of 1913 Dr. Castle obtained from a fancier in England two pairs of black-eyed white mice. These he kindly handed over to me for investigation. From the outset the progeny of these mice proved to be extremely healthy and vigorous.

1. *Black-eyed White Crossed Inter Se*

This cross gave two distinct classes of young, black-eyed white and "piebald." The distinction between the two classes can best be shown by the tabulation of their progeny on the basis of the amount of dorsal pigmentation they possess. I have for some time estimated the per cent. of the dorsal surface pigmented in the case of all spotted animals recorded. This gives a basis for classification which, though it may at first glance seem to be inexact, nevertheless has been shown by comparing the

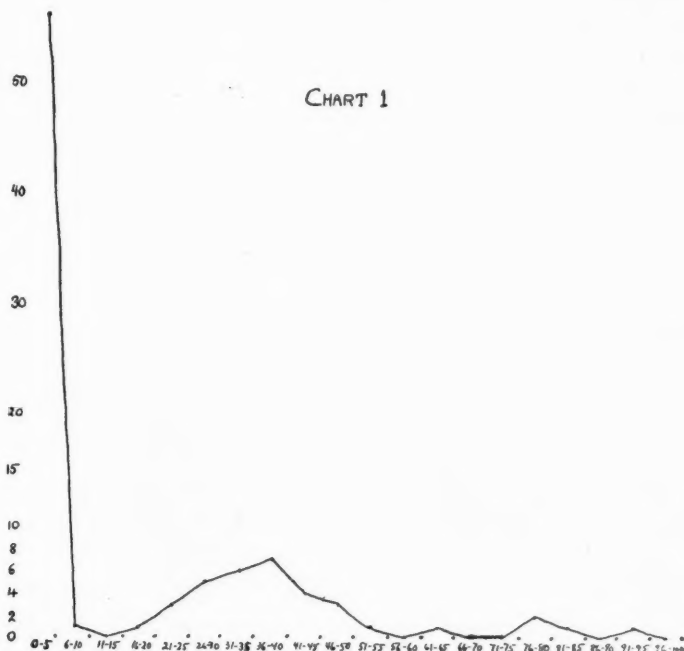
estimates of two or more investigators on any one animal to be surprisingly exact and fully as satisfactory as any other system of grading.

TABLE I.

Type of Cross	Per Cent of Dorsal Pigmentation															
	0-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80
Black-eyed white <i>inter se</i>	56	1	0	1	3	5	6	7	4	3	1	0	1	0	0	2
Black-eyed white × piebald.....	105	0	0	1	1	12	8	11	5	6	4	4	1	3	4	9
Piebald × piebald.....	0	0	0	0	0	4	6	7	13	6	2	9	4	6	2	5
Total.....	161	1	0	2	4	21	20	25	22	15	7	13	6	9	6	16

From Chart I it will be seen that 44 of the 75 young obtained fall in the class between 0 and 5 per cent. of dorsal pigmentation. These are the black-eyed whites.

60



The remaining 31 young are more or less scattered along the range of "piebald" forms. The gap between the two classes is a considerable one and is certainly significant.

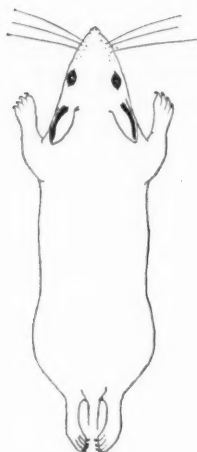


FIG. 1

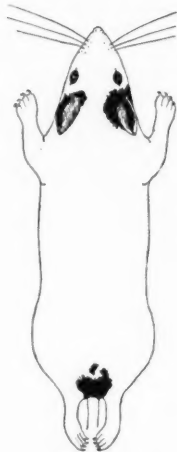


FIG. 2

Figs. 1-4 are diagrammatic and are intended to show the two groups of spotted animals. Figs. 1 and 2 show

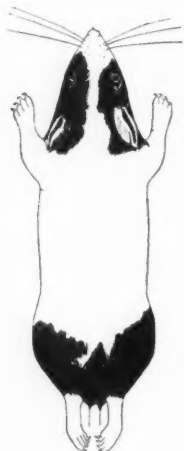


FIG. 3



FIG. 4

the common range of variation within the black-eyed white type and Figs. 3 and 4 the same for the "piebald" type.

2. *Black-eyed White* \times *Piebald*

This mating brought out two interesting facts. *First*, all black-eyed whites behaved in essentially the same way, approximately an equal number of black-eyed white and piebald young being produced. *Second*, the same distinctness between the two types held good, as will be seen from the chart given below (solid line).

3. *Piebald* \times *Piebald*

Piebald animals from black-eyed white parents and from the cross of piebald \times black-eyed white were mated *inter se*. They produced only piebald young, 93 in number.

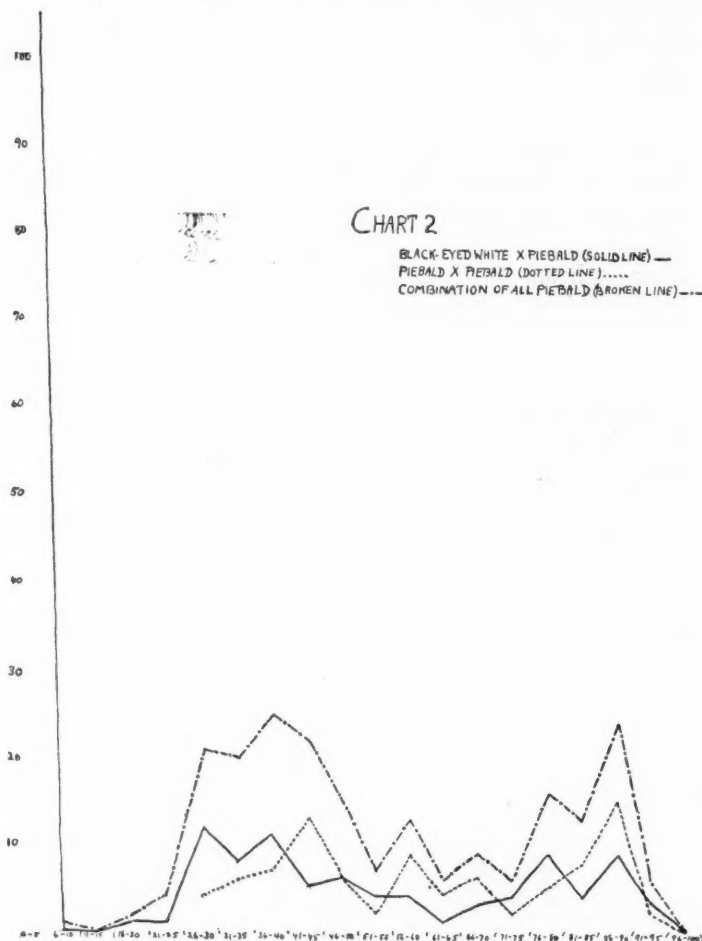
The distribution of these young according to the degree of dorsal pigmentation they possessed is shown by Chart 2 (dotted line).

It will be noticed that there is no approach to the black-eyed white condition (0-5 per cent.). There are also indications of two main modal points, one at 41-50 per cent. and one at 80-90 per cent. A complete curve formed from the sum of all piebald animals included in Table I, is given in Chart 2 (broken line).

This further emphasizes the bi-modal nature of the curve in the case of piebald mice and makes it seem likely that there are two genetically distinct grades of this variety. It is hoped that opportunity will arise in the future to investigate this point more accurately.

4. *Discussion*

From the three types of matings given above the following facts may be deduced: (1) The inheritance of the characters in question is alternative, not blending in nature; (2) black-eyed white is epistatic to ordinary piebald spotting.



The behavior of black-eyed whites in crosses 1 and 2, Table I indicates that they are always heterozygous dominants and that they can not, therefore, be obtained in a condition to "breed true."

With this in mind it is interesting to calculate the expected ratio when black-eyed whites are crossed *inter se*. If black-eyed white is due primarily to a dominant factor

which obeys the ordinary laws of mendelian inheritance, we should expect that black-eyed whites would be obtained of two genetic types, homozygous and heterozygous. If now black-eyed whites were mated together at random, the matings should be either (1) $DD \times DD$, (2) $DD \times DR$ or (3) $DR \times DR$. In the case of (1) and (2) only black-eyed white young should be produced, while type (3) should give approximately 3 black-eyed whites to one piebald. Random matings would therefore produce a ratio of black-eyed whites to piebalds considerably in excess of 3:1.

If, on the other hand, the DD form of black-eyed white mice behaves in a fashion similar to the homozygous yellow mice, failing to develop, we should expect a ratio of 2 black-eyed whites to one piebald young, no matter what the origin of the black-eyed white parents might be, whenever two black-eyed whites are bred together.

The results are as follows:

<i>Black-Eyed White \times Black-Eyed White</i>		
	Black-eyed White	Piebald
Observed	57	39
Expected 2:1 ratio	64	32
Expected 3:1 ratio	72	24

When one realizes that the ratio in one case should be considerably *higher* than 3:1, it seems that the results indicate a 2:1 ratio and the heterozygous nature of black-eyed whites.

To further test this hypothesis individual tests of twenty-one black-eyed whites coming from black-eyed white parents were made by crossing with piebald animals. If the DD combination is possible, approximately seven of the twenty-one tested should be of that constitution. All of them, however, proved to be heterozygous. While the numbers should be supplemented by further tests, they are certainly sufficient to serve as a basis for a tentative conclusion that black-eyed white mice are always heterozygous.

The numbers from the cross of piebald \times black-eyed white are more extensive and closely approximate a 1:1 ratio. The numbers obtained are 105 black-eyed whites and 102 piebald, while the 103 of each would have been exactly an equality ratio.

The behavior of the piebald animals when crossed *inter se* is exactly what would be expected if piebald was hypostatic to black-eyed white and distinct from it in inheritance.

The next question to be considered is the relation of black-eyed white to "self" or solid coat, in inheritance.

RELATION OF BLACK-EYED WHITE TO SELF

A preliminary investigation of this question has been made. The "self" race used was really technically not a "self" but genetically it carried neither the black-eyed white nor piebald spotting factors. Somatically the self race used was a "blaze" race of the type which I have previously put on record. Further crosses which I have made between black-eyed whites and true selfs have shown, even in early stages, clear evidence that the behavior of the blaze and true self races is directly comparable.

1. "Self" \times Black-eyed White

The F_1 generation produced by crossing self (blaze F6B) animals with black-eyed whites consists of two very distinct forms. These have been produced in a ratio of 50 Type "A" to 47 Type "B." The first of these, Type "A," is shown in Fig. 5. While the percentage of dorsal pigmentation of this type is subject to some variation (see table), it will be noticed that they are ordinarily between 80 and 90 per cent. colored. The spots of color

Type "A"	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100
Black-eyed white \times self (blaze)	0	1	2	0	1	1	2	0	9	15	10	8	1

appear to have slightly more irregular and less clearly defined outlines than do those of the ordinary piebald mice and many of the spots are distinctly smaller in size (compare Figs. 3, 4 and 5). Just how much of this ap-

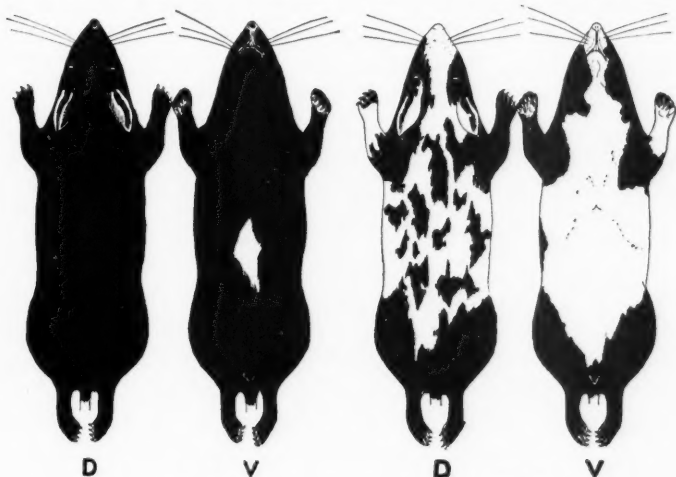


FIG. 5

FIG. 6

pearance is due to true genetic difference between the two types of spotting is of course problematical and must remain so until a larger mass of data is available.

Concerning class "B" (Fig. 6) little need be said save that they appear in every way identical with heterozygotes ordinarily obtained in a cross between "self" and "piebald" animals. They vary from entirely solid colored animals to those having approximately 20 per cent. of the *ventral* surface white. They may be tabulated as follows:

	Per Cent of White on Ventral Surface						
	0	1-5	6-10	11-15	16-20	21-25	26-30
Type "B"	5	23	8	3	2	1	0

2. Type "A" Animals Crossed Inter Se

Type "A" animals obtained in F_1 are distinctly "spotted." They have a clearly discernible amount of white

and are not in the least like heterozygous "selves" of any recorded type. When crossed together they give three somatically distinct classes of young, "self," "piebald" or like class "A," and black-eyed white. The numbers obtained are 15 "self," 31 spotted (piebald or like class "A") and 11 black-eyed whites.

3. Type "A" \times Piebald

To test them further type "A," animals of this class were crossed with homozygous piebald mice extracted from the black-eyed white crosses. Again three general classes of young were obtained as follows: 45 "self," 54 spotted (piebald or like type "A") and 29 black-eyed whites.

4. Type "B" \times Piebald

To compare the behavior of types "A" and "B" this cross was made. Only two classes of young resulted as follows: 82 class "B" and 78 piebald. No black-eyed whites were obtained.

Discussion

The question now arising is whether the factors for self, black-eyed white, and piebald are allelomorphic or independent in inheritance.

From the nature of the F_1 generation it is certain that the black-eyed white animals are forming two kinds of gametes in respect to their spotting factors.

If now the conditions "self" coat, "black-eyed white" and "piebald" are all related as members of a system of triple allelomorphs, we can express the cross as follows:

S = self factor.

W = black-eyed white factor.

sp = piebald factor.

Then

	S	S	=	self	\times	W	sp	=	black-eyed white
gametes	S					W			
						sp			

F_1 Generation	S	W	=	Type A, Fig. 5
	S	sp	=	Type B, Fig. 6

If now animals of Type A are bred *inter se* we should expect

- $$S | W \times S W$$
- 1 SS = self
 - 2 SW = like Type "A"
 - 1 WW = (not formed because homozygous)

The one WW individual could not be formed since by experiment it has been shown that W can exist in only one of the two gametes forming a zygote. When W meets S, an animal like Class A is produced, when it meets sp a black-eyed white results.

The expectation therefore is that, if a system of triple allelomorphs is operative here, we should have *no black-eyed whites formed from mating together class "A" animals.*

The result of this mating quickly settles the above hypothesis for 15 "self" colored, 31 spotted (like or nearly like Type "A"), and 11 black-eyed whites have been obtained.

It is clear, therefore, that "black-eyed white" depends upon a factor which is at least partly independent of that producing "piebald" spotting. Let us suppose that this is the case and that "black-eyed whites" always carry piebald in all of their gametes and an epistatic inhibiting or restrictive factor producing increased whiteness in one half their gametes. If W equals restrictor and w its absence and sp equals the factor for piebald spotting, all black-eyed whites will be Wwspsp, in zygotic formula and will form two sorts of gametes, Wsp and wsp.

This will account for the results in mating black-eyed whites *inter se* due to the failure of the WWspsp zygote to continue its development because of the double dose of W.

If now black-eyed whites Wwspsp are crossed with selfs wwSS, two classes of F_1 zygotes will result, WwSsp and wwSsp. The former will produce a new zygotic combi-

nation really differing from the black-eyed whites in the substitution of a "self" bearing gamete for a "piebald" one in the zygotic formula. The result is an animal like Type "A," Fig. 5; Type "B," Fig. 6 shows the other F_1 type which is entirely free from the W factor and which is merely a heterozygote between "self" and "piebald."

If class "A" animals are crossed *inter se* we should on this new hypothesis expect the following results.

1	WWSS	not developed
2	WwSS	very dark spotted
2	WwSsp	not developed
4	WwSsp	like parents (type "A")
1	Wwspsp	not developed
2	Wwspsp	black-eyed white
1	wwSSp	"self"
2	wwSsp	"self" or "self" with white ventral patch (type "B")
1	wwspsp	"piebald"

Four of the 16 zygotes in F_2 would have two doses of W and would not develop. Of the remaining 12, seven would have some degree of white spotting depending upon whether they were WwSS, WwSsp or wwspsp in formula; three would be "solid" colored or like type "B" of F_1 and two would be black-eyed whites.

On this hypothesis the F_2 generation would be as follows:

	Observed	Expected
Solid	15	15
Spotted	31	35
Black-eyed whites	11	10
	<u>57</u>	<u>60</u>

A further test of the nature of type "A" is possible. If they are bred to piebald animals, four classes of young should result as follows.

WwSsp	like class "A"
Wwspsp	black-eyed whites
wwSsp	solid colored
wwspsp	piebald

Lumping together the WwSsp and the wwspsp animals

we should have 2 spotted, 1 black-eyed white and 1 self. The results are as follows:

	Observed	Expected
Spotted	54	64
Self	45	32
Black-eyed white	29	32
	<u>128</u>	<u>128</u>

Whether the excess of "self" animals is significant is, of course, a question to be borne in mind but it is extremely doubtful whether it is due to anything more than a chance deviation.

Type "B" animals have, upon mating with "piebald" individuals, given very close to the expected ratio of 1 type "B" to 1 "piebald." The exact numbers are 82:78; expected ratio 80:80.

IS BLACK-EYED WHITE IN MICE AN ALLELOMORPH OF ALBINISM?

The experiments of Castle and Wright have shown that a dark red-eyed variety of guinea-pig exists which is an allelomorph of dilute pigmentation and of albinism. This possibility in the case of mice is eliminated by crossing black-eyed white with albino, when on the supposition that the condition found in guinea-pigs holds true in mice all the young should be either black-eyed white, albino or dilute pigmented. Actually there were obtained from a single mating of this sort five young, all intensely pigmented, two blacks and three browns; thereby eliminating the possibility that black-eyed white, in mice, is an allelomorph in the albino series.

CONCLUSIONS

The fact that black-eyed white spotting in mice appears to be due to a factor independent of and supplementary to the factor for "piebald" spotting leads to interesting speculation as to the nature of spotting and

indicates that spotting in mice is dependent upon more than one pair of clear-cut mendelizing factors. Modifying factors which may be more or less difficult to analyze but which nevertheless are certainly present, contribute to the extent of variation in spotted races.

"Blaze" or forehead spotting is apparently independent of ordinary "piebald" spotting, as I shall hope to show in a future paper; "black-eyed white" is primarily due to an independent genetic factor and "piebald" makes a third independent type. If now in the "piebald" stock there exist at least two genetic races as are indicated by the curve of all piebald animals obtained in the "black-eyed white" crosses, the condition is still further complicated. At all events one can truthfully say that the distribution of pigment occurring as it does along a series from "self" colored to "black-eyed white" animals, offers a field for the activity of many mendelizing factors. There is no *a priori* reason why this should not be true, there are many experimental reasons steadily increasing why it appears to *be* true.

Spotting in rodents is tempting as genetic material because of the clear patterns and contrast between colored and white areas. It is, however, *as a character* extremely sensitive to minute quantitative and qualitative changes and its apparent genetic simplicity is a snare and a delusion.

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THE F_1 BLEND ACCOMPANIED BY GENIC PURITY

A DESCRIPTION OF MECHANICAL CHARTS FOR ILLUSTRATING
MENDELIAN HEREDITY IN EACH OF THREE WELL-
KNOWN CASES OF BLENDING INHERITANCE IN
THE FIRST HYBRID GENERATION

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THE mechanical charts herewith figured are the first of a series prepared for the purpose of presenting graphically and schematically the established facts of heredity. These particular mechanisms, illustrating blending inheritance, consist essentially of wooden slabs on which the gametic formulæ of the several generations are charted—those for P_1 and F_2 are written on flat surfaces, while that for F_1 is inscribed on cylinders which turn freely. A capital letter represents a gene; the corresponding small letter the absence of that gene. The location of genes, whether they lie in the same chromosome *i. e.*, are linked, or in different chromosomes, is shown graphically by placing their symbols in the same or in different squares, or upon the same or different half-cylinder surfaces. In each of these selected cases the individuals of the P_1 generation are homozygous in respect to both of the traits or allelomorphic phases concerned. The genes contributed by the P_1 generation to the F_1 zygote are charted on the starred faces of the freely turning cylinders. The back of each spool contains the same inscription as the face of its partner cylinder. Each face of a cylinder represents a chromosome—the two faces the two chromosome types in reference to the

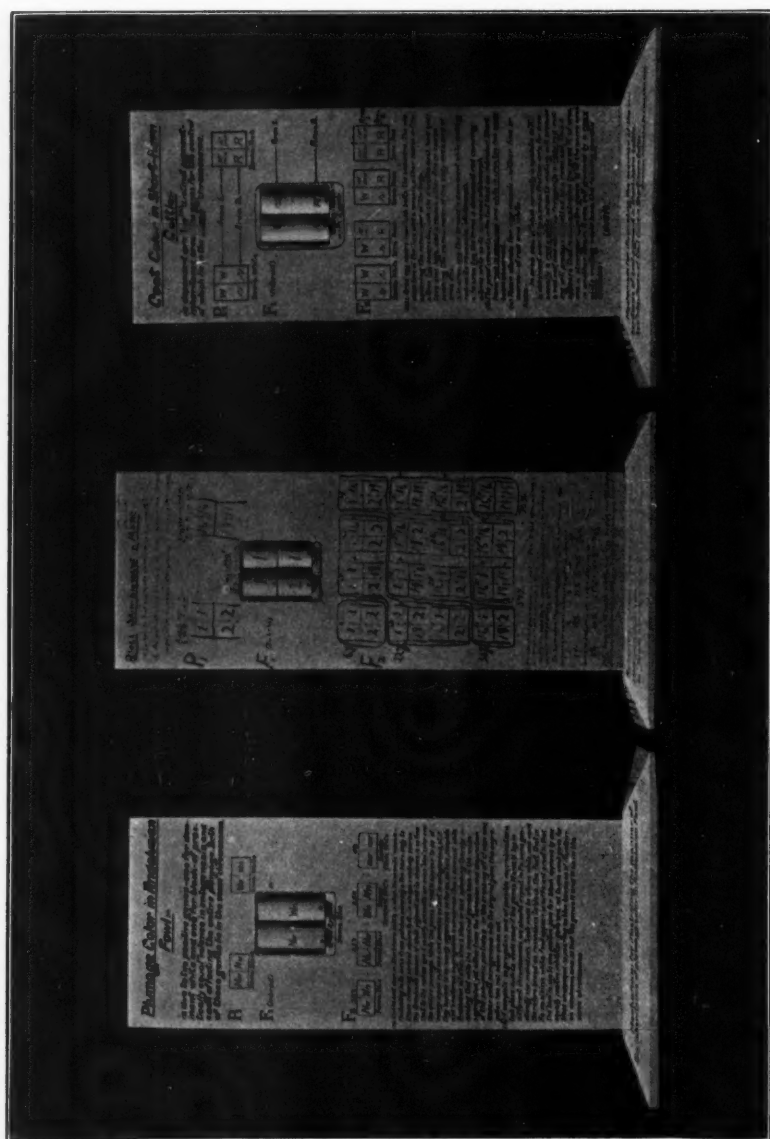


FIG. 1. Three Mechanical Charts demonstrating Mendelian Processes in Cases of Blending Inheritance

traits lying in that particular chromosome, which each F₁ individual as a parent is capable of passing on. Therefore, by turning the spools so that all possible combinations are made, one can read off directly all of the different hereditary potentialities to be had by inbreeding the F₁ generation. Consequently the F₂ line (which is charted on a flat surface) is simply a record of such combinations.

For the purpose of this study a case of blended inheritance is one in which the development in F₁ of a given somatic trait—regardless of whether it develops from one or more genes—is about midway between its development in the two parents, each of which is of pure stock in reference to the trait concerned. Until about the year 1910 students of heredity were unable to coordinate the general rule of dominance and segregation on one hand, with the frequent exception of blending and segregation on the other. Now the existence of at least three different routes by each of which nature arrives at the somatic blend in F₁ are recognized, and each finds ready interpretation in consonance with the theory of the pure gene. The first of these is the dilution or true blend route, by which nature appears to travel in the classical cases of the Blue Andalusian¹ fowl resulting from the crossing of splashed-white and black parents, and of the pink four o'clock (*Mirabilis jalapa*) resulting from the crossing of red and white parents.

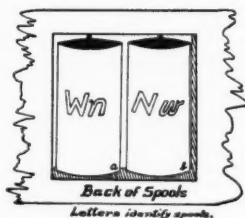
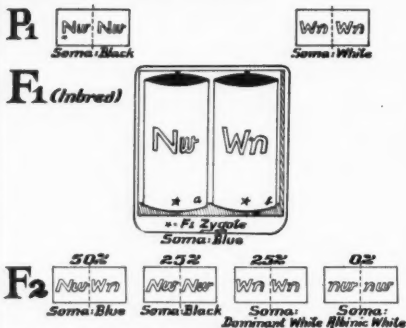
The ordinary mode of inheritance is strongly duplex—that is, the zygote normally possesses two genes for each trait, either one of which genes is usually sufficient—with possibly a liberal surplus of valence—to give full somatic expression to its correlated trait. In such cases complete dominance in F₁ and clear-cut segregation in F₂ are the rule. Occasionally, however, in cases wherein a duplex parent possesses a strong somatic development of a trait,

¹ "Mendel's Principles of Heredity" (3d Impression, 1912), p. 51, by W. Bateson.

Plumage Color in Andalusian

Fowl:-

is due to two positive genes—one for dominant white and one for black—of practically equal valence in ontogenesis, and each affecting the entire plumage. Both of these genes lie in the same chromosome.



(a) Unlike coat color in Short-horn cattle in which the somatic mosaic-fluctuating in its areas from patches covering a few hairs only to those covering several square feet—is always relatively coarse, the Andalusian mosaic of black pigment and its absence is so fine, that to the naked eye it usually presents an even blue color over the entire plumage. While the genes N and W appear to be of nearly equal valence and somatic extent in ontogenesis, still they appear to be loosely organized so far as certain, complete and unaltered segregation is concerned. Thus a dominant white Andalusian will often show a black or blue splashing thereby indicating that while the ancestral genes have in the main segregated, yet either from the adhesion and disjunction of the sub-genic particles or the breaking off of new and lesser units homogeneous with the original gene, the segregation has not been clean cut.

(b) If complete segregation and all possible recombinations took place such as would occur if the genes N and W lay in different chromosomes, we should expect in F_2 some genetically nur individuals. Such would be albino white, and would therefore breed as recessives to black. The fact that in F_2 no albino white fowl appear is sufficient proof (1) that the blue is due to one positive gene for black opposed by one equally positive inhibitor-gene and (2) to one weak gene for black unopposed appearing as blue because of its intrinsic weakness, and (3) that the genes N and W lie in the same chromosome.

* N (nigrum) i.e. black

Mechanism for Illustrating the Manner of the Inheritance of Plumage Color in Andalusian Fowl.

FIG. 2. Chart showing the F_1 Blend Associated with Genic Dilution—the True Blend

a single gene—from the paternal or the maternal line only—for such trait, in the zygote, is not sufficient to give a somatic development of the trait equal to that possessed by the duplex parent. In such cases, therefore, the unit trait in question is blended in the F₁ soma—a case of imperfection of dominance.² Nevertheless, in such cases segregation is just as clean-cut in the germ-plasm as it is in the cases accompanied by strong somatic dominance.

In Andalusian fowl “W”—dominant splashed-white—and “N”—(nigrum) black—are two opposing and allelomorphic genes of nearly equal valence in ontogenesis. Their combination and interaction determine plumage-color in the offspring. The black Andalusian is duplex for black plumage-pigment, while the splashed-white is duplex for dominant splashed-white. The F₁ offspring are “blue”—a shade really intermediate between the white and the black. Moreover, the genes “W” and “N” evidently lie in the same³ chromosome. The evidence for this consists in the fact that in the F₂ generation, resulting from inbreeding two blue Andalusians, neither albinic white nor jungle⁴—pure or modified—patterned fowl result, which would be the case if “N” and “W” lay in different chromosomes, permitting, in some F₂ zygotic combinations, the elimination of both “N” and “W.” For further explanation of this particular type of blended inheritance see the accompanying figure descriptive of the mechanical chart “Plumage-Color in Andalusian Fowl.”

The second type—that of multiple factors—is typified by the inheritance of black skin-pigment in man. It is a matter of common knowledge that a mulatto of the first generation is about intermediate in density of black skin-pigment between his white and his black parents. In 1913

² “Imperfection of Dominance,” *American Breeders Magazine*, No. 1, Vol. 1, p. 39, 1910, by C. B. Davenport.

³ “Heredity and Sex,” p. 93 et seq. (Columbia University Press, 1913), by Thomas H. Morgan.

⁴ “New Views about Reversion,” *Proceedings of the American Philosophical Society*, Vol. XLIX, No. 196, 1910, by C. B. Davenport.

Black Skin-Pigment in Man.

1. Is due to two segregable genes in each gamete.
2. The potentiality of each gene finds measurable somatic expression, regardless of the presence or absence of other genes.

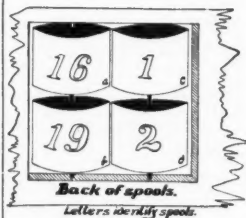
A white man
6% N in skin.

A negro woman
70% N in skin.

P ₁	1 1	A mulatto 38% N in skin.	16 16
	2 2		19 19

F ₁ (Inbred)	1	16
	2	19

* = F₁ Soma -



G ₁	1 1 6 6	1 1 23 23	1 16 14 14	1 16 38 38
	2 2	2 19	2 2	2 19
G ₂	1 1 23 23	1 1 46 46	1 16 36 36	1 16 65 65
	19 2	19 19	19 2	19 19
G ₃	16 1 2 2	16 1 36 36	16 16 2 2	16 16 55 55
	19 2	19 19	19 2	19 19
G ₄	16 1 36 36	16 1 55 55	16 16 2 2	16 16 70 70
	19 2	19 19	19 2	19 19

* = Somatic types not found in P₁ or F₁. - Gametic types not found in P₁ or F₁. N = Black skin-pigment.

The figures indicate the pigment producing power (in percent) of their respective genes.

In Bermudian (Negro-white) families Davenport found five frequency maxima in density of skin-pigment.

1 2 3 4 5
5%N 18%N 33%N 46%N 70%N
same maxima in above scheme -
6%N 23%N 36%N 55%N 70%N

In F₂ there are 45 possible gametic matings, in pure races the density of black skin-pigment varies greatly, hence the seemingly unmanageable complex.

Mechanism for illustrating the manner of the inheritance of black skin-pigment in man.
See Heredity of Skin Color in Negro-White Crosses - Davenport 1913.

FIG. 3. Chart showing the F₁ Blend Associated with Multiple Factors for One Somatic Trait

Dr. C. B. Davenport⁵ found, by analyzing data on the family distribution of black skin-pigment measured quantitatively (by the color-top) among the mixed white-and-black families of the Island of Jamaica, the Island of Bermuda, and in our own Southern States, (1) that black skin-pigment in man is the somatic working out of two segregable genes in each gamete, and (2) that the potentiality of each gene finds definite measurable somatic expression, regardless of the presence or absence in the zygote of other genes. Now these two genes appear to be of different valence; they appear also to lie in different chromosomes. The scheme outlined by the mechanical chart "Black Skin-Pigment in Man" is quite consonant with the facts of inheritance which Dr. Davenport found in nature. The facts seem to be that in white persons one of these genes will develop from practically none to about 1 per cent. of blackness in skin-color, and the second from very little to about 2 per cent., thus resulting in a blackness of skin-color of 6 per cent. or less in the somas of members of the light races. He found that some races of negroes show about 70 per cent. black in skin-color. In such races one gene for black skin-color seems to be potential to developing approximately 16 per cent. of black skin-color, the other about 19 per cent. The evidence that there are two such genes, and that they are segregable, *i. e.*, that they lie in different chromosomes, and that their values among the strains studied are about as described above, lies in the fact that, in the hybrid families in Bermuda, Davenport found 5 frequency maxima in intensity of black skin-pigmentation, and that his analysis of the family distribution of this trait, quantitatively measured in many mongrel families of known pedigree, demanded the existence in nature of the scheme above outlined.

Darwin, whose method of study was essentially observational, knew that the F₁ generation was quite generally

⁵ "Heredity of Skin-Color in Negro-White Crosses," published by the Carnegie Institution of Washington, 1913, by Charles B. Davenport.

remarkably uniform, but among and beyond the F_2 general observation found no rule of inheritance. It remained for the application of the analytical or Mendelian study to discover order in the apparent somatic tangle of F_2 . The skin-color story just related is a striking case in point.

The third class of blended inheritance—the particulate or mosaic—is typified by the behavior in heredity of coat-color in short-horn⁶ cattle in which, in the F_1 soma, the



*The red of these scales is carmine which according to Ridway's Color Standards is composed 55% of spectrum red, 45% of black.

FIG. 4. Composition of Skin-pigmentation in Representatives of Three Races.

Jamaicans—Employees of the Moneague Hotel, Moneague, Jamaica.

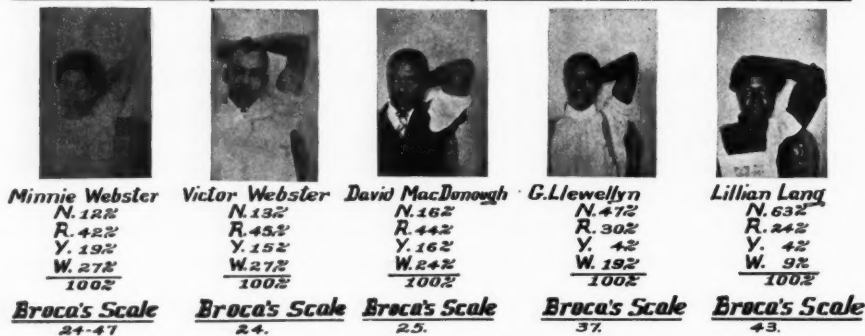
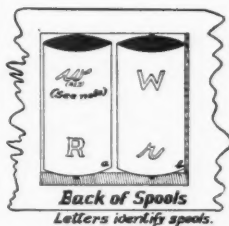
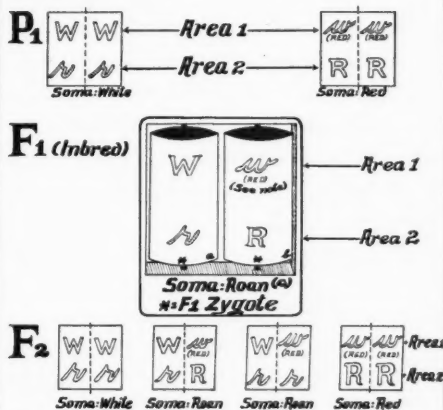


FIG. 5. Variation in Skin-pigmentation Among Jamaicans

⁶ "Inheritance of Coal-Color in Short-horn Cattle," AMERICAN NATURALIST, December, 1911, January, 1912, by H. H. Laughlin.

Coat Color in Short-horn**Cattle:-**

is dependent upon two distinct pigment inheritance areas the genes for the control of which lie in the same^(a) chromosome.



- (a) Area one covers two flank belts, the underline, the median line of the face, and a mosaic, either coarse or fine, covering the remainder of the body.
- (b) Area two covers the neck, the sides, the back, hind quarters and legs, and a mosaic either fine or coarse, covering the remainder of the body exclusive of area one.
- (c) In area one the breed is dominant white covering red as its recessive allelomorph. (See note)
- (d) In area two the breed is dominant red covering albino white as its recessive allelomorph.
- (e) The proof consists in the fact that an individual Short-horn red in area one and white in area two has never been observed.
- (f) Roan stands for any mosaic—either fine or coarse—of red and white.

Note:-

In area one "W", which normally is epistatic to R, is dominant over it by a small fraction only, for occasionally a red x white somatic mating will produce a red calf, and about as frequently a red x red mating will produce a spotted or a roan calf. Thus it appears that in some strains the gene R of area one is stronger than the gene W of the same area in another strain. A red calf produced by a red x white mating would have the following gametic formulae:

Area one WR-opposing positive genes allelomorph.

Area two R-R-a positive gene and its absence allelomorph.

The scheme herewith described, including this occasional variation in the relative valence of the allelomorphous genes for area one so that the end result of their intra-zygotic reaction is a fluctuation thru the critical point of somatic dominance, accounts for practically all of the observed facts in connection with inheritance of coat-color in Short-horn cattle.

Mechanism for Illustrating the Manner of the Inheritance of Coat-color in Short-horn cattle. See "Inheritance of Coat-color in Short-horn Cattle"—American Naturalist, Dec. 1911, Jan. 1912.

FIG. 6. Chart showing the F₁ Blend Associated with Particulate Inheritance—a Patent Mosaic

character concerned is, in its grosser aspect, clearly midway between the corresponding traits of its two parents, although a closer inspection reveals a mosaic the elements of which are the parental traits quite unchanged. The difference between the Andalusian fowl and the short-horn cattle cases seems to be as follows: In the Andalusian each gene influences the entire plumage-color, and appears to be struggling unsuccessfully, as it were, for the supremacy in somatic expression, thus resulting in a very fine and quite generally distributed blend or mosaic; while in short-horn cattle the controlling genes are double the number, each pair being confined to specific coat areas in somatic expression, and the resulting mosaic, although quite variable in coarseness, is always relatively coarse and is also quite definitely patterned.

Thus, normally (for the exception see the note in Fig. 6) in Area 1 the gene "W" is clearly dominant over the gene "R." In Area 2 the gene "R" is dominant over its absence. There seems to be in Area 2 no competing or allelomorphic gene whatever—it is simply "R" or its absence, *i. e.*, albinic white; whereas in Area 1 the "W," which is epistatic to "R," will leave "R" by its absence. The evidence for all this consists in the fact that a *white short-horn* (which is evidently dominant white, always duplex, in Area 1, and always recessive white in Area 2) will, when crossed with a black Angus, which is *dominant black for its entire coat*, give in the offspring a calf *dominant white, simplex, in Area 1, and black, simplex, in Area 2*—the familiar "blue roan" in cattle. That in short-horn cattle the genes "W" and "R" lie in the same chromosome is sufficiently proved by the fact that the color pattern is *never* reversed, that is to say, in *bi-colored individuals of whatever coarseness of mosaic, Area 1 is*

(Note:—When this paper on coat-color was written it was pointed out that coats red in Area 1 and white in Area 2 were *never* observed. Now the modified interpretation, involving linkage and a variation in genic valence, as explained in the text and Fig. 6 of the present article, accounts for practically all of the observed facts.)

always dominant white, and Area 2 is always red, and we never find an individual red in Area 1 and white in Area 2, although solid whites and solid reds, and bi-colored individuals of the first specified type are common. The reversed pattern, i. e., red in Area 1 and white in Area 2, would occur if the genes "W" for Area 1 and "R" for Area 2 were completely segregable, i. e., if they lay in different chromosomes. For a further explanation of this mode of blending inheritance see the accompanying chart, "Coat-color in Short-horn Cattle."

THE POPULATION OF THE "BLANKET-ALGÆ" OF FRESHWATER POOLS¹

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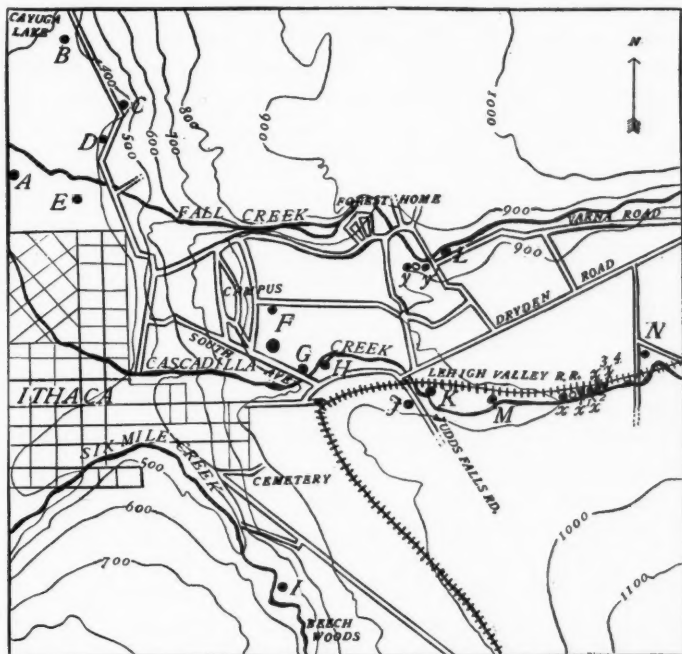
THIS is a study of the community of life that is bound up with the floating masses of filamentous algæ, popularly known as "blanket-algæ." An acquaintance with this population is worth cultivating for the sake of the variety, beauty and interesting peculiarities of the plants and animals found in this unique habitat. It may be of utilitarian value as well, for there exists a relation between plankton production, algal growth and fish culture. Furthermore, it may be a help to students and to teachers of biology when they are in search of certain laboratory materials, which in these algæ masses flourish.

Method of Collecting.—A fine silk hand net of No. 12 bolting cloth was used to lift the algæ from the surface of the water. The largest collection covered about 2,800 sq. cm.; the smallest about 10 sq. cm., but most of them were from 200 sq. cm. to 800 sq. cm. in area. Doubtless, many active and comparatively large foraging animals, such as small fishes or adult insects, escaped while the net was surrounding and enveloping the mass. Probably comparatively few of the smaller forms were lost through the fine silk mesh of the net. The volume of the mass was then computed in cubic centimeters. As the mass sometimes lay in thin layers and sometimes in thicker masses, the proportion of volume to surface was seldom the same. About 200 cu. cm. was the average. The components of the "blanket" were determined and all forms, plant and animal, were listed and their size and relative abundance noted. The collections were made during the fall and early winter of 1912 and the spring and early summer of 1913.

Location and Character of the Pools.—The pools are all located in the vicinity of Cornell University campus at

¹ This study was carried on in the limnological laboratory of the department of entomology of Cornell University under the direction of Professor James G. Needham.

Ithaca, N. Y. (see map). They varied from shallow, transient collections of ditch-water to large, permanent, usually stagnant pools. Those lettered *B*, *C*, *D*, *G*, *J*, *M*, and *N* belong to the first category. Pools *x*, *x*¹, *x*², *x*³, *x*⁴,



Pools in the Vicinity of Cornell University Campus.

and *y*, *y*¹, *E*, *K*, *I*, and *L* are permanent pools and measure from four to thirty or more inches in depth. Pool *H* is a quiet part of a large stream. Pools *F* and *A* are artificially enclosed and are filled from pipes. The pools of the lowland of Cayuga Valley (about 400 ft. above sea-level) are *A*, *B*, *C*, *D*, and *E*. The others are among the hills (about 800 feet above sea-level).

The Filamentous Algæ of the Floating Mass.—Although there was such variety in seasonal conditions and in the

location and character of the pools, nevertheless some forms appeared constantly. Among the filamentous algæ, *Spirogyra* was almost uniformly present, appearing twenty-eight times out of thirty. The species were not identified until March, but in the twenty collections taken in the spring and early summer, the most frequent species was *Spirogyra varians*. *Spirogyra insignis* was found five times. Other species seen less frequently were:

<i>S. tenuissima</i>	<i>S. communis</i>
<i>S. sticticum</i>	<i>S. fluviatilis</i>
<i>S. grevilliana</i>	<i>S. bellis</i>
<i>S. weberi</i>	<i>S. nitida</i>
<i>S. quinina</i>	<i>S. inflata</i>
<i>S. crassa</i>	<i>S. decimina</i>
<i>S. majuscula</i>	<i>S. rivularis</i>

Usually the masses contained several species of *Spirogyra*, often with a large proportion of one species, and the *Spirogyra* was almost invariably associated with other filamentous algæ. Among the most frequent of these were *Mougeotia* and *Zygnema*. *Vaucheria* was found frequently in the autumn and early winter. *Oscillatoria* was quite constant after its first occurrence in early March, but it was usually in very small quantities. *Ulothrix Draparnaldia* and *Microspora* were seen occasionally, but not in abundance, while *Anabæna oscillaroides* was found only once. In general, the large permanent pools produced the greatest variety of genera and species of these algæ, but otherwise there was no apparent relation between the genera of algæ produced and the character and location of the pools; with the possible exception of *Draparnaldia plumosa*, which was found four times out of five in shallow ditches.

Diatoms, Desmids and Other Algæ.—Diatoms were invariably present. Of these, there were four that were constant and always in greater quantity than other kinds. These four were *Navicula*, in great variety, *Synedra*, *Cocconeia* and *Gomphonema*. Other diatoms were seen ir-

regularly as to quantity and time of occurrence and included the following:

<i>Tabellaria</i>	<i>Cocconeis</i>
<i>Fragillaria</i>	<i>Campylodiscus</i>
<i>Meridion</i>	<i>Amphora</i>
<i>Asterionella</i>	<i>Pleurosigma</i>
<i>Diatoma</i>	<i>Nitzschia</i>
<i>Encyonema</i>	<i>Odontidium</i>
<i>Cymbella</i>	<i>Cyclotella</i>

Most of these were free but often *Gomphonema*, *Cocconeis* and *Cymbella* were in colonies attached by branched or simple stalks to larger forms. *Encyonema* is found end to end in colonies enclosed in long filament-like gelatinous envelopes. *Navicula* as well as stalked diatoms sometimes covered the bodies of larvæ and smaller crustaceans and also the cases in which the chironomid larvæ spent part of their time. Variation in occurrence of diatoms is apparently due to seasonal changes, which will be considered later.

Other algæ were less constant, the most regular one being *Closterium*, which occurred in eight collections, showing a number of species. Of the other desmids that appeared, *Cosmarium*, *Penium* and *Staurastrum* were usually in small quantities. Twice, however, *Cosmarium* and *Closterium* both appeared in abundance, the first time being in a permanent but shallow pool (I) where *Ulothrix* predominated, and the second time in a shallow but probably permanent roadside pool (G) covered with *Spirogyra*. The Volvocaceæ were represented by *Volvox*, *Eudorina*, *Pandorina*, *Sphærella* and *Chlamydomonas*. Two Phæophyceæ, *Dinobryon* and *Synura*, and four Protococcaceæ, *Dictyosphaerium*, *Kirchneriella*, *Protococcus* and *Scenedesmus*, added variety but did not appear frequently. *Peridinium*, *Pediastrum* and *Ophiocytium* were rare.

The pools (L and Y) that had the greatest variety in desmids and kindred forms were also rich in diatoms.

These pools are large and one or two feet deep and have thin mud overlying rock bottom. Both lie near Fall Creek.

The pools (K , x , x^1 , x^3 , x^4) near Cascadilla Creek presented the only specimens of *Dinobryon* that were seen. These pools are permanent and deep and have stony bottom.

It may be significant that in the low-ground pools there were few kinds of diatoms and in only one such pool (A) were there any desmids.

The Animal Population.—The floating and entangled vegetation of these masses supports a large animal population. The protozoans found were particularly varied and interesting. *Ameba*, *Arcella* and *Diffugia* appeared irregularly in the upland pools. *Cochliopodium* and *Mastigameba* were rare. No other Rhizopods were observed. The ciliates were not determined before March, with the exception of *Paramecium*, which was listed from the first. In the twenty collections made since March first, fifteen genera of ciliates have been observed. *Paramecium* was constant and abundant. Among the larger representatives of the group, *Coleps*, *Chilodon*, *Colpidium*, *Stylonychia* and *Vorticella* appeared frequently and in large numbers. *Stentor*, *Dipleurostyla* and *Amphileptus* were less frequent, as were the smaller members of the group, namely, *Euplotes*, *Halteria* and *Askanasia*. *Coleps* was especially noticeable in pool y^1 , while *Vorticella* was plentiful in pools D and G . Pools D , G and J , which supplied the largest number of genera and of individual ciliates, are shallow ditch-pools with muddy bottom, while A and Y in which smaller numbers were found, but still many genera, are larger and deeper, but have muddy bottom or muddy water. From this it seems evident that these protozoa prefer water with inorganic material in suspension, although they are said to avoid water polluted by decaying organic matter. These tiny creatures forage busily among the algal filaments, some swimming and rotating smoothly, others, such as *Halteria* and *Stylonychia*,

moving by jerks and sudden dartings hither and yon. The minute form, *Euplotes*, has a peculiar method of locomotion that looks like walking along a filament, though it is merely forward progress by means of cilia.

The flagellates were represented by *Euglena*, *Distigma* and *Phacus*, of which the first was fairly constant. Three heliozoans, *Actinosphærium*, *Actinophrys* and *Vampyrella*, appeared infrequently. *Hydra* was found in one collection only, and no other cœlenterates were seen.

Various worms, mainly the microscopic nematodes as well as unidentified planarians and turbellarians, also three kinds of oligochætes, namely *Nais*, *Tubifex* and *Chaetogaster*, were frequent but not regular inhabitants of the alga-mass.

The rotifers were regularly a part of the population, furnishing species of eighteen genera. Determination of genera was not undertaken until March. The genus most constantly in evidence was *Diglena*, especially in dirty water, foraging industriously, nibbling and pulling at the algæ. A species of *Metapidia* with a broadly curved lorica was seen several times. It clung by its toes to debris, while the flow of water carried food-particles past the rotating cilia into the mastax. *Anurea*, *Salpina* and *Synchaeta* were found exclusively in the pool nearest Cayuga Lake, pool A. Also in this pool, as well as elsewhere, were found *Polyarthra*, *Rotifer*, *Adineta*, *Diglena*, *Notholca labis* and a long-spined species of *Rattulus*. This permanent pool and a similar pool (X¹) of the highland were richest in rotifer life. Forms found in the latter pool and not observed elsewhere, were *Notommata* and a species of *Stephanops* with a fan-like anterior projection of the lorica. Other genera identified were *Brachionus*, *Philodina*, *Mytilina*, *Mastigocerca* and *Diaschiza*. *Chaetonotus*, a representative of the *Gastrotricha*, was seen a few times.

The Gastropoda, the only mollusk group represented, did not furnish a constant element, since only eight collections contained any snails. *Lymnea* appeared once,

Physa five times and *Planorbis* four times. These snails varied in size from two to twenty-five mm. long. Except in one instance, they were in shaded pools or came out on cloudy days. The exceptional case may be considered as similar because the luxuriant growth of watercress near the algae furnished spots of shade, although most of the "blanket" was in sunlight. It seems fair to assume that snails are not regular inhabitants of the surface algæ, but merely forage there when there is little or no sunlight.

Many small crustaceans were observed. *Chydorus* and *Bosmina* were numerous, while two other Cladocera, *Daphnia* and *Simocephalus*, were less in evidence. The ostracods found were in eleven collections and quite numerous. They have not been identified. *Cyclops*, *Canthocamptus* and *Diaptomus* were the copepods identified. *Cyclops* was remarkably constant and abundant. Many females bearing paired egg-sacs and many copepod nauplii, presumably young cyclops, were among the number. The adults were from one to three mm. long. The Isopod, *Asellus aquaticus*, was found only once and then in a mass of algæ close to a mud bank. Two amphipods, *Gammarus* and *Hyalella*, were observed several times.

The last group of foraging animals and the one to which the largest individuals of this population belong is the Insecta. In this class were found larvæ, nymphs and adults, representing five orders of insects. Three nymphs of *Callibaetis*, in pool A, one of *Bætis*, in pool M, and ten of undetermined genera of *Ephemerida* in Pool F were the only may-fly nymphs found. The *Odonata* were more frequent. There were a few Libellulids, and a number of nymphs of *Enallagma* and *Ischnura*. The Hemiptera had only one representative, *Corisa*, the water-boatman, which was caught twice but was frequently seen swimming on the clean surface of the pool. It can hardly be considered a regular inhabitant of the alga-masses.

Four different larvæ of the order Diptera made up the greater part of the insect population. *Chironomus* was particularly conspicuous, since the larvæ were found con-

stantly, and were generally very numerous. Masses of eggs of *Chironomus cayugæ* Johannsen were found enclosed in an oval mass of gelatin anchored to some of the algæ, also myriads of newly-hatched, almost microscopic larvæ were seen, so it is reasonable to assume that, for these pale pink or yellowish chironomus larvæ (1-18 mm. long), this environment is the normal one. A few larger species, some of them blood-red, were found also. Larvæ of the "punkie" *Ceratopogon* and of the soldier-fly, *Odonotomyia*, were seen occasionally. Although mosquito-larvæ are found regularly in stagnant pools, it is surprising to note that only twice were these larvæ found among the filaments of the floating algæ. These larvæ were not identified.

A few larval beetles and a few adults made infrequent appearances. Undetermined *Hydroporus* and other dytiscid larvæ were among these. Although known as a dweller among filamentous algæ, the Haliplid beetle larva, *Peltodytes*, was seen only once, its long spiny hairs tangled in the vegetation. Adults of two genera of Hydrophilid beetles were identified as *Helophorus* and *Crenophilus* and a few other diving-beetles were seen but not identified.

Although tadpoles, and once a young salamander, were found in the collections, they can hardly be reckoned as members of the society under consideration.

Dominant Forms.—In this diverse population the constant and abundant forms have been few. *Spirogyra*, especially *Spirogyra varians*, *Mougeotia* and *Zygnema*, were the principal constituents of the "blankets." Among the Diatoms, the dominating forms were *Cocconeia*, *Navicula*, *Gomphonema* and *Synedra*. Other algæ were best represented by *Closterium*, *Dictyosphaerium* and *Dinobryon*. Among the animals *Paramecium*, *Euglena* and the rotifer, *Diglena*, were quite constant. The forms that appeared most regularly were *Cyclops* and the larvæ of *Chironomus*. Some of the less constant forms showed the influence of seasonal variation.

Seasonal Variation.—In the autumn and early winter *Vaucheria* was usually present, but appeared only twice in the spring. *Pandorina* and *Peridinium* also appeared late in the year. At that time fewer protozoa were seen than in the spring, but, as has been said, variations here seem to be more closely related to the character of the water than to the temperature. *Gammarus* and the nymphs of may-flies and dragon-flies were most numerous in October, November and December.

The spring season also had its special forms. *Oscillatoria* appeared first in March and was constant thereafter. Diatom production was at its height in April and May at water-temperatures varying between 8° and 16° C. and there was a marked decline in diatom appearances toward the end of June. In contrast to diatoms, desmids seem to require higher temperatures, since most of the *Closterium* and all of the *Cosmarium* and *Staurostrum* that were seen appeared in June, in water at temperatures between 15° and 20° C. The proportion of *Dinobryon* in collections became noticeably greater during the latter part of June. The smaller crustaceans, excepting the ever-present *Cyclops*, showed marked increase in numbers as well as in diversity during May and June. The same seasonal increase was noticed for *Anguillula* and the rotifers. Most of the coleopterous and dipterous larvæ were found in May and June, except *Chironomus* which was present at all seasons.

Another point of interest in connection with seasons is the time of reproduction. *Spirogyra* was found conjugating in October, April and June; *Mougeotia* in November, December, May and June. Young, sessile plants of *Ulothrix* were seen in April and May. All through the year, copepod nauplii and female *Cyclops* bearing egg-sacs were observed. *Chironomus* eggs were found in April and early in June, while very young larvæ were abundant during April, May and June.

In view of the fact that floating algæ were found in large quantities in December, even under ice, it was sur-

prising to find some of the pools totally devoid of this kind of vegetation in spring. Pools *K*, *M*, *x*, *x*¹, *x*², *x*³, *x*⁴ showed this peculiarity. Their "blanket-algæ" did not reappear until May. This disappearance of surface vegetation may have been due to spring freshets, as the pools mentioned are in the flood-plain of Cascadilla Creek, although not in the stream-bed.

The Natural Balance.—Like other societies, the population of the "blanket-algæ" has its producers and its consumers, its hunters and its hunted, each readily exchanging rôles as occasion demands. The synthetic organisms include with the phytoplankton a few chlorophyll-bearing organisms of the zooplankton; that is, forms like *Euglena*, *Phacus* and *Distigma*, which, in sunlight, have the holophytic method of feeding (Stokes, 1895). Diatoms require nitrates, silica and some salts to make their dainty and beautifully marked shells. Since they are comparatively heavy, they sink slowly, but are brought to the surface during the spring and fall circulation of the water. In spring they multiply rapidly near the surface, since they need oxygen and sunlight.

Many of the tiny creatures, including ciliates, *Cladocera*, rotifers and nymphs and larvæ of some insects are in search of diatoms. These animals eat other tiny food particles as well as diatoms. The rhizopods, *Arcella* and *Ameba*, ingest diatoms, desmids, small protozoans and even rotifers. *Vampyrella* consumes the cell-contents of algæ. *Actinophrys* prefers the spores of algæ, but takes small protozoa. *Actinosphærium* is omnivorous (Stokes, 1895). Many of the ciliates eat diatoms and other ciliates. The food is drawn into the oral opening by means of currents of water which are directed toward the opening by the constant motion of cilia. One ciliate, *Chilodon*, has a peculiar method of feeding. It protrudes a broad flexible lip-like expansion of the anterior end and gathers up food particles with a sweep of this organ.

Turbellarian worms feed on rhizopods, ciliates and rotifers. Rotifers eat diatoms and some nibble algæ,

whereas the closely related *Gastrotricha*, *Chaetonotus*, eats minute particles of decayed animal and vegetable matter, rarely taking diatoms.

The smaller crustaceans in general and the snails are scavengers, removing decaying algæ and bits of dead insects or other animal matter. The Cladocera, however, are said to eat diatoms and many of the smaller algæ. Ostracoda are omnivorous and often attack their own species.

Among the insect members of this society, the larvæ of the may-flies and midges are the great herbivores, although, in addition to algæ, diatoms and leaves of higher plants, consuming a great variety of vegetable substances, both living and dead. The great abundance of *Chironomus* larvæ make this genus an important factor, both as a consumer, and as food for other animals. *Chironomus* larvæ and pupæ are, in turn, eaten by dragon-fly nymphs, and other predaceous larvæ. They are of much importance as fish-food.

Dragon-fly nymphs are predatory. Some species eat back-swimmers and water-boatmen, small crustaceans and snails, coleopterous and dipterous larvæ and even young dragon-fly nymphs. The larger nymphs are eaten principally by fish, occasionally by water-birds.

This brief account of some of the feeding-habits will serve to show how much all the members of this society are dependent upon the others, and, at the same time, are in constant danger of extinction. Each form acts as a check upon too rapid multiplication of some other form. Since the most prolific animals in this population are *Cyclops* and *Chironomus*, each must have peculiarities that enable it to survive in this environment and to compete with other animals. *Cyclops* adapts itself easily to changes. Its prolific reproduction, seasonal constancy, and plasticity, give it great advantage over other small crustacea. *Chironomus*, also constant, prolific and adaptable, finds abundant food and comparative shelter among the algal filaments.

SHORTER ARTICLES AND DISCUSSION

ON PRACTICAL VITALISM

IN a series of critical and polemical essays, published during the past few years in American journals by diverse authors, particularly by Jennings, the problem of vitalism has been discussed in a manner that may seem exhaustive.

There would appear to be no possibility of adducing new arguments in the matter. If in spite of this a new presentation is here attempted, it is because the author holds a standpoint entirely divergent from what has been thus far set forth in the discussion.

If it is true that the argumentation of the promoter and leader of the new scientific vitalism—Driesch—becomes at times somewhat metaphysical, it appears to me also that the criticism, as made by Jennings, tends at times to become dialectical and sophistical.

I can not otherwise characterize the tendency to efface any specific difference between the living and the non-living. By isolating at random a feature of the living and comparing it with an inorganic model one can indeed seem to show the identity of the two. But in this procedure we recognize the typical method of the ancient sophists. I can find nothing of interest, for example, in such an argumentation as the one cited below from Jennings.¹

In a rejoinder to Lovejoy, who insists "that the same phenomena occur in a given organism in spite of profound modifications of the composition and configuration of the parts" Jennings objects that we have here

a proposition that holds for things in general. An iron body of a certain form moves toward the earth. We may change the form in most varied ways . . . change the material, substitute lead, brass, stone . . . ; it still moves toward the earth.²

Nothing is easier than to prove that black and white, plant and animal, man and monkey, are "fundamentally the same."

¹ A typical one for the antivitalistic criticism.

² AMERICAN NATURALIST, 1913, p. 395.

But does an affirmation of this sort annihilate in any way the specific difference between man and monkey, or diminish the interest of science in this specificity?

The innumerable attempts of the critics of vitalism to prove by comparison of certain isolated features that the living is nothing more than an extreme complication of the non-living fail, because the analysis in such cases is never exhaustive. One may prove that living and inorganic coincide in many points; he can not prove more.

I do not see why these points of coincidence are of more importance and interest for our conception of the matter than the points of undeniably distinctive difference, even though the latter are as yet unanalyzed.

The best way to test the validity of an idea or hypothesis is to follow it to its most extreme but logically inevitable consequences, taking these as a statement of the proposition involved.

If we follow this method in order to obtain an objective and exact formulation of the essence of vitalism (or of its antithesis, mechanism), we can say that what mechanism asserts is this: Whenever a certain configuration of matter occurs or is given, there also what we call "life" is found; or in more popular terms, the artificial production of a living organism from "non-living" matter would theoretically be possible.

Vitalism, on the other hand, is a standpoint that in last instance denies such a possibility.

It is clear that both the assertion and the negation are unprovable, and as such are matters of faith, not of empirical science.

If one attempts to give an estimate of the two from the standpoint of science, sympathy must, it appears to me, incline to the vitalistic view, since scepticism is the very palladium of exact science.³

It is generally overlooked that if one of the two opponents is to be reproved as aggressive, that one is the mechanist rather than the vitalist. The mechanist in asserting that he knows more than can be proved is filled with a scientific optimism of a somewhat frivolous character.

Yet it is the moderate agnostic standpoint, declaring no belief

³ It may be objected that a negation is dogmatic to the same degree as an assertion. This may be true. But one can replace the term "negation" by some other less radical expression, such as "doubt," without altering the essence of the standpoint.

in the possibility of artificial synthesis of the living so long as that is not proved, that is subjected to ridicule as a dogmatic, obscurantist and non-scientific doctrine.⁴

The entire problem to me falls in the domain of "Natur-philosophie," that branch of our knowledge which can not directly prove the truth or logical necessity of the results of investigations made in its field; can do no more than to make them plausible; and thus give to us a genuine sensation of mental satisfaction.

There is no intention here of participating in the endless dispute above sketched; I do not know what could be added in this direction, from a vitalistic point of view, to the formulations of Driesch.⁵ Our purpose is the defense of the right to a *practical vitalism*, as a method of exact empirical (although not necessarily experimental) investigation.

We do not care whether the methods demanded by such a vitalism are or can be proper also for inorganic investigation.

It appears that they are not, for the mechanists oppose their "veto" in the name of exact science to all constructions of the vitalistic system, even though not fully analogous with that which will be detailed below.

Practical vitalism claims the right to be restricted in formulating hypotheses only by postulates of logic and of the general theory of knowledge, and by nothing else.

⁴ The same point can be made with regard to the other aspect of vitalism—the so-called "experimental indeterminism." As to this, it must be admitted that the empirical evidence seems to favor the vitalistic standpoint. The assertion of the mechanists, that experimental indeterminism can not hold for the living, is likewise a matter of faith, and the burden of proof falls upon those who make it.

⁵ I must nevertheless confess, despite my profound admiration for Driesch's work, that I find that his chief experimental foundation of vitalism, by means of his masterly analysis of certain cases of regulation, fails to produce the desired effect; chiefly because the entire argument rests upon certain experiments that are, as one may say, a lucky chance in biological investigation. It would be quite possible that no organisms having the marvelous powers of regulation and equipotentiality shown by *Tubularia*, the sea-urchin or *Clavellina*, should ever be discovered. Can it be admitted that a scientific proof of vitalism as the basis of biological research would therefore remain inaccessible? The argument in such a capital problem must, I think, rest on a more general basis, one resulting from an adequate analysis of essential and genuine vital phenomena. I incline therefore to consider Driesch's further analysis, as presented in his "Science and Philosophy of the Organism" as a no less valuable part of his work.

We hold as a justified demand of the theory of knowledge that every hypothesis must be fruitful; that is, it must give a number of deductions that can be verified empirically. Every hypothesis which permits us a prediction is to be considered a step in the progress of knowledge, until such time as it is replaced by a new one, more suitable or more fruitful.

Biological, and particularly embryological, investigation needs sometimes to introduce as a hypothesis for the explanation of certain empirical facts the idea of so-called "immaterial" (or in Jennings's terminology "non-perceptual") factors.

This is the chief point on which are based the recriminations of most critics of vitalism, especially of Driesch's vitalism.

The belief in such "non-perceptual" factors is in Jennings's mind synonymous with obscurantism or dogmatism. To Ritter "the vitalism . . . is the belief that organic phenomena can not be fully explained by referring them to the material elements of which organisms are composed, but that something *not really belonging to the natural order* [?] . . . is present in living things" (italics mine).

To me it is entirely obscure why the term "non-perceptual factor," employed by Jennings in a logical and consistent manner, is by him rejected as nonsense.

His formulation of the non-perceptual is very clear.

Conditions subject to diverse physical tests will here be called either perceptual or physical.⁶

A non-perceptual agent would be one which though producing at a particular time a particular physical event, was not subject to other physical tests for its presence.⁷

I have given a formulation much resembling this, of what I call the "immaterial factor" in my paper bearing that title, printed in the "Festschrift für Schwalbe."

This work was to have been published the first of August, 1914, at the very moment of the outbreak of the war. Whether it has been issued I do not know.

My definition is as follows:

Als materiell gilt uns im allgemeinen ein Objekt unserer Erkenntniss welches eine Mehrzahl von einander unabhängiger Eigenschaften (sc. Wirkungsweisen) in sich vereinigt und sowohl in Tätigkeit als in Ruhe befindlich wenigstens gedacht werden kann.

⁶ Johns Hopkins University Circular, 1914, No. 10, p. 8.

⁷ *Ibid.*, p. 12.

Ein zur Erklärung bestimmter Wahrnehmungen ersonnener Factor von dem eine derartige Annahme d. h. ein Zustand der Nichtbetätigung widersinnig wäre mag folgerichtig als "nicht materiell" bezeichnet werden.

Neither Jennings's "non-perceptual" or my "immaterial" can be considered an illogical or contradictory conception. Criticism must, so far as my own doctrine is concerned, be therefore concentrated solely on the strength of the empirical foundation for the hypothesis of immaterial factors in any given case.

Besides the logical definition given above, an examination is required of the question; What exactly can be meant by, or *how can one be led to assume, an "immaterial factor" as a result of experimental investigation, or at least as a hypothesis impelled by such a result?*

To Jennings the assumption of a "non-perceptual agent" leads directly to, or is synonymous with, the so-called "experimental indeterminism," as admitted by Driesch.

He seems to neglect every other possibility of the action of an "immaterial factor." I do not see that this is inevitable.

To me the essential point of the problem lies in the question of the "bearers" for any sort of empirically detectible action (induction, force, or the like).

Suppose that it were found that the factors directing the movements of a given element of a living organism (for example, the cell of an embryo), in a given direction *m* to the point *n*, lie outside itself.

We will then assume at the point *n* a center of forces.

Suppose now that we can deduce from this assumption certain consequences that will be subsequently verified empirically.⁸ Our assumption that gives us possibilities of prediction becomes then a scientific reality. We say "reality," although it may remain somewhat hypothetical. We find the same condition of affairs in the imperceptible but strongly inferred realities of physics, etc.

⁸ I find that there is a point at which Jennings's conception of the "non-perceptual" seems to lead us wrong. It is well to say with Jennings that such an agent is one producing at a particular time a particular physical event *but not subject to other physical tests for its presence* (italics mine). But Jennings seems not to take into consideration that a "particular physical event" or a "single mode of action" (in my formulation) can lead to many empirically verifiable consequences.

Suppose now that at the point of space where we have projected the center of forces there lies some element of the embryo, such as a cell. The scientific routine will call this element the "bearer" of the forces in question.

But it is also possible that no element and no matter is to be found at this point.

The first impulse will be to search for some other element of the embryo, situated elsewhere, that can act as such a center, by irradiating certain "lines of force," which influence in some manner the movements of the first considered element. We will, however, assume a case where no such element acting at a distance can reasonably be supposed. What now?

If the fundamental assumption holds true, that the factors determining the movements of the element lie outside of itself, we find ourselves confronted by the following alternative:

Either the presumed factors have a bearer that is not cognizable, or they have no material bearer at all!

It is clear that if we deny the existence of bearers that are evidently perceptible, we can also exclude the possibility that such bearers exist, but are invisible owing to their minuteness; for the presumed center of forces lies according to our assumption outside the organism; or in a district of it where there is no formed embryonic matter at all.

Thus under the circumstances our two alternatives signify the same thing, for to say that there is a bearer of factors that is cognizable solely as the factors themselves involves a tautology; an assumption of the sort so well characterized by the French as a "*hypothèse gratuite*." While any one is free to make such an assumption, no scientific use can be made of it. Methodologically it is perhaps comparable to Kant's "*Ding an sich*," which likewise must remain without empirical content.

As a fundamental postulate of biological (and especially of embryological) research, there can therefore arise the conception of factors which, although spatial and localized in space, have no material bearers, and as such may be denominated immaterial.

Is such an idea indeed nonsense; something that proves the obscurantism of its promoter?

I am well aware that the "immaterial" factor here presented is far from coinciding with Driesch's *Entelechy* or with any

analogous agent that is *e definitione* not solely immaterial, but also non-spatial.

If the entire weight of antivitalistic criticism is directed and concentrated wholly against such ideas as that of Entelechy; and if the mechanist will agree with me that a spatial localization of a center of forces may be assumed without necessarily combining this with a material bearer, I shall be much gratified. But I fear that this is not the case. The "dynamical præformation of the morphe," as I have elsewhere called the immaterial but spatial factors of morphogenesis,⁹ must, I fear, fall under the same anathema as the classical vitalism.

To resume the chief postulate of my own "vitalism": if morphogenetic investigation is led in a rigorous inductive way to assume a spatial factor at a definite point inside or outside the embryo, no difficulty or contradiction or nonsense arises if no "embryonic" matter, or what is the same, no material "bearer" for this factor can be found at that point. Yet of course no one can be prohibited from forming any sort of hypothesis as to such functionless bearers. It may be even a psychological necessity to form such hypothesis, for we love a "Ding an sich." But such will form no part of empirical research.

The right to work with such immaterial factors, and in the inductive way set forth above, is, for me, the essence of *practical* vitalism.

We have now to examine consequences and postulates derived from our fundamental assumption, which seem to present very great difficulty. If we admit a dynamical factor localized in space but not derived from a material bearer, it will be asked, whence comes and how arises this factor?

The question of causation is based on a postulate of knowledge that can not be eluded; it must be answered in some manner.

I will attempt to point out briefly how one can think the origin or evolution of such an immaterial morphogenetic factor, although it must be insisted that we have here a problem which does not stand in immediate connection with the purely empirical method of investigating the factors considered, so to say, *per se* in their activity.

I see no difficulty in assuming an immaterial causality; that is, the arising of an immaterial factor having a certain property

⁹ *Biologisches Centrblatt*, Bd. 32; *Archiv. f. Entwicklungsmechanik*, Bd. 39; *Festschrift für Schwalbe*, 1914.

(for example, configuration) from another less complicated immaterial factor, and so on.

The chain of immaterial factors could in this manner logically be pursued backward to the beginning of the embryogenesis, or to the egg.

As to the relation of such immaterial factors to Driesch's entelechy, they can be ranged solely in the category of "means" (Mittel) of the latter for the purpose of morphogenesis.

But I repeat that this is for me a matter belonging for the present not to experimental investigation, but to the domain of "Naturphilosophie."

If it appears as if I agree in this point with the "standpoint of radically experimental analysis" of Jennings, this is not really the case. The latter author seems to reject all that does not belong to experimental investigation.

I think, on the contrary, that vigorously logical considerations, deductive and even inductive, on the given empirical data form a legitimate and integral part of our science of nature.

A. GURWITSCH

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